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Long-term Osprey (*Pandion haliaetus*) Population Dynamics in Relation to Food Web Change at Flathead Lake, MT

by

Brandon E. Jackson

B.A. Colgate University, 1999

Presented in partial fulfillment of the requirements

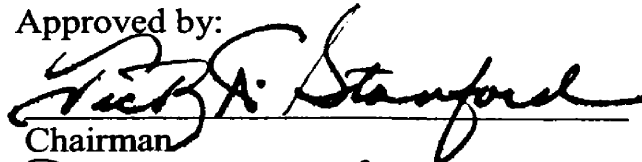
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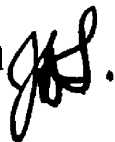
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Long-term Osprey (*Pandion haliaetus*) Population Dynamics in Relation to Food Web Change at Flathead Lake, MT

Director: Jack A. Stanford 

After beginning to recover from DDT, which nearly exterminated many raptors worldwide, the Osprey (*Pandion haliaetus*) population at Flathead Lake was subjected to a large experiment caused by the 1981 arrival of the introduced opossum shrimp (*Mysis relicta*). Subsequent to the introduction, the majority of the fish biomass in the lake shifted from pelagic surface-feeders (i.e. westslope cutthroat trout, kokanee salmon) to non-native, deep-water foragers (i.e. Lake Superior whitefish, lake trout). Detailed productivity and foraging studies of the Osprey population in the 1960-70's provide a unique opportunity to examine effects of this change in the food web on the main apex piscivorian. Nests and fledglings were counted, and prey remains examined, during the nesting seasons of 2001-02. The number of productive nests increased from a low of less than ten in the early 1970's, to a high of 61 in 2001. The number of fledglings increased from 68 in 1979, to 131 in 2001. The post-*Mysis* Osprey diet included more lake trout and northern pikeminnow, and less largescale suckers compared to pre-*Mysis*, and no cutthroat trout compared to 9 % in 1969-70. These trends reflect the changes in available fish as demonstrated by floating gill net data.

Preface

This thesis is divided into two chapters. The first chapter is a broad literature review of Osprey ecology and the species' interactions with humans around the world and at Flathead Lake, Montana. The introduction to the second chapter may seem somewhat redundant. This is because the second chapter was written to be a stand-alone manuscript to be submitted to a journal. At the time of this printing, I am in the process of choosing a journal.

I took on this project after an offer from Dr. Charlie Blem and Leanne Blem, of Virginia Commonwealth University, to be part of their larger scale, and longer term, study of the Osprey population at Flathead Lake. As principal investigators, while they played no official role in my academic pursuits, they secured funding and volunteer field crews through the Earthwatch Institute. Because my study fit into the larger one, and I did not have independent funding, my methods were constrained by the needs of the larger project. Nevertheless, with a detailed historical data set and large field crews under the direction of two accomplished PI's, I was able to produce an analysis that is more in-depth than most two-year masters degree projects.

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Chapter 1: Review of Osprey Ecology

Ospreys (*Pandion haliaetus*), unique fishing raptors, are one of the most cosmopolitan birds in the world, breeding or wintering on every continent except Antarctica. In the 19th and early 20th centuries, Osprey populations declined due to habitat loss, campaigns that exterminated Ospreys as pests or competitors for fish, or collection of eggs/nestlings for pets. Populations were further reduced or exterminated by loss or change of fisheries, and low hatching rates from pollution (especially the organochloride pesticide DDT; e.g. Ames & Mersereau, 1964). However, since the 1970's when DDT, hunting, and collecting were banned, they have reestablished populations around the world often using artificial nesting platforms where natural nest sites were not previously available (Poole, 1989). In this chapter, I review Osprey ecology, focusing on three factors that influence Osprey abundance and success: prey availability, nest site availability, and seasonal human disturbance (Vana-Miller, 1987, Poole, 1989).

Prey Availability

Ospreys stoop onto prey items feet first like all other accipitrids. However, they are the only birds in the world that forage for fish by diving completely under water, grabbing the prey item with their feet (Bent, 1937; Poole, 1989). Other raptors [e.g. Bald Eagles (*Haliaeetus leucocephalus*)] also stoop feet first but rather than diving into the water, they pull fish off the surface with their feet. Non-raptorial piscivorian birds (e.g. Sulidae) dive head first into the water, grabbing fish or other prey in their bills.

Fish usually make up all of an Osprey's diet, though small rodents, snakes, and birds may supplement fish (Poole, 1989; pers. obs.). Chubbs and Trimper (1998) found that 12.5% of the diet of five nests was composed of small passerines and mammals.

When foraging, Ospreys soar 10-200 m above the water (Dunstan, 1974; Poole, 1989). They dive either from a soar or from a hover, which can increase their foraging success (Grubb, 1977a). The Osprey plunges headfirst, swinging its feet forward at the last instance to enter the water feet and head first, usually diving less than one meter (Poole et al., 2002). After floating back to the surface, the bird orients the fish so that the fish's head points forward. This foraging technique requires two elements for the prey to be available to the Osprey: the Osprey must be able to see the fish from the air, and the fish must be in the top meter of the water column.

Evidence for the effect of weather on foraging success is inconclusive. Weather conditions did not affect prey delivery rates (Stinson et al., 1987), and Flemming and Smith (1990) found that cloud cover did not affect foraging success. Grubb (1977b) found that wind velocity had no effect, however sun occlusion (i.e. cloud cover) and rippled water decreased foraging effort. Stinson (1978) found a correlation between wind gustiness and foraging trip length.

Ospreys forage in virtually all aquatic and inshore marine habitats (Greene, 1987; Poole, 1985, 1989; Flemming & Smith, 1990). In fact, many coastal Ospreys will fish both ocean and inland freshwater in the same day. Usually, Ospreys are non-selective foragers. Their diet reflects the relative percentages of the size and species of the fish community that is available to them (e.g. Dunstan, 1974; Edwards, 1989; Carss & Godfrey, 1996). However, foraging strategies may be different for Ospreys nesting in

dense colonies, where prey is patchily available, as described by the Information Center Hypothesis (ICH, Ward & Zahavi, 1973). Greene (1987) demonstrated that Ospreys cued in on individuals that returned to the colony with schooling prey species, and then attempted to find the school. Otherwise, the Ospreys fished for more evenly distributed species.

Nest Site Availability

Ospreys historically built nests at the top of the tallest dead trees, or the tallest live trees with dead tops, in the area (Swenson, 1981). In North America, Ospreys have chosen a wide variety of tree species including white and red oak (*Quercus spp.*; Ames and Mersereau, 1964), live cyprus (*Taxodium spp.*, Hagan, 1986), ponderosa pine (*Pinus ponderosa*), and cottonwood (*Populus trichocarpa*, pers. obs.). Ospreys also nest on cliff walls and pinnacles in canyons (Swenson, 1981), on the sea shore (Poole, 1989), or even on the ground of some predator-free islands (Ames and Mersereau, 1964).

The creation of reservoirs in the 20th century initially provided numerous dead trees and abundant fisheries that boosted Osprey populations in some areas. Henny et al. (1978) found 47% of Osprey nests in Oregon associated with reservoirs. The eventual decay without replacement of those snags then led to local population declines (Ewins, 1997; Mace et al., 1987).

As part of Osprey recovery efforts in the past 30 years, wildlife managers and property owners have installed platforms on the tops of telephone poles or dead trees. In some cases, these artificial nests sites are preferred by Osprey, and can have higher productivity than natural nest sites, possibly due to increased stability during extreme weather (Ames and Mersereau, 1964; Austin-Smith & Rhodenizer, 1983). Additionally,

Ospreys have nested on buoys in bays (Bent, 1937), low goose platforms, railroad bridge trestles, central pivot field irrigators, cupolas, and cellular phone towers (this study).

Nests do not have to be at the prey source, but Osprey do prefer to nest, and productivity is usually highest, near water (Ewins, 1997); most nests are within one km of the water's edge, and no more than about 15 km away (Poole, 1989).

A more subtle, yet critical, element for Osprey nesting is a perch site for the male. Males require a perch, on which to rest outside of the nest, within sight or sound of the nest (Vana-Miller, 1987).

Seasonal Human Disturbance

Ospreys are very tolerant of high levels of human disturbance, but can be sensitive to seasonal activity (Ames & Mersereau, 1964). If there is human activity around a nest site upon return from wintering grounds in the spring, the Ospreys pay little attention to the disturbance. For example, Ospreys nesting on a railroad bridge never showed any signs of agitation when large trains passed just beneath them on a regular schedule (pers. obs). However, if that activity level increases suddenly after nesting has begun, the female can become excited and leave the nest in defense, potentially crushing eggs or nestlings in the process (Ames and Mersereau, 1964), and leaving them exposed (Reese, 1977). When incubation coincides with arrival of vacationers, Ospreys nesting in popular vacation areas are vulnerable to such problems, which can decrease productivity (Swenson, 1979a).

Osprey Decline and Recovery

Osprey populations around the world saw their most serious declines from the start of the 20th century to the mid-1970's. The most severe declines were caused by DDT and other pesticide contaminations (Ames & Mersereau, 1964; Henny & Wight, 1969; Poole, 1989). Additionally, loss of habitat by deforestation and shoreline development of lakes, oceans, and rivers reduced suitable nesting habitat. Increased commercial fishing and fisheries management disrupted food webs. Ospreys were even considered pests or competitors for fish in some areas of the world, and were subject to deliberate extermination campaigns.

Due to bioaccumulation, concentration of contaminants may be high in apex predators. For birds at the top of the food web, most notably Bald Eagles and Ospreys, DDT contamination caused decreased shell thickness and increased the occurrence of crushed and addled eggs. The resulting lower productivity led to substantial population declines continent-wide (Ames & Mersereau, 1964; Poole, 1989). Low hatchability was the limiting factor in the Flathead Lake, MT, Osprey population (MacCarter, 1972a). DDT was banned continent-wide in the mid-1970's. Many populations across the country began recovering quickly (e.g. Henny et al. 1977; MacCarter & MacCarter, 1979), with annual population increases of 6-15 % across the continent (Ewins, 1997).

The widespread population increases can also be attributed to legislative changes protecting Ospreys and Osprey habitat, and the increased availability of artificial nest structures (Poole, 1989; Ewins, 1997). Logging and development have resulted in forests with fewer large old trees, in which Ospreys prefer to build nests. Nevertheless, nest numbers have grown because Ospreys have increasingly used artificial structures,

whether or not intended for that purpose (Ewins, 1997). Bioaccumulation of pesticides, nest availability, and human persecution are *usually* no longer limiting factors on most Osprey populations in North America.

Need for New Research

Deliberate and accidental introductions of species and the associated changes in food webs have had widespread, mostly negative, effects on native species and their ecosystems worldwide (Mooney & Hobbs, 2000). Many studies have described direct influences of non-native introductions either on competing native species, or on predator/prey interactions. For example, in many midwestern streams, native brook trout have been replaced by non-native brown trout (Moyle et al., 1986). However, more recent studies have demonstrated effects of species introductions cascading across multiple trophic levels. For example, Olenin and Leppakoski (1999) showed that introduced mollusks have altered entire benthic communities in the Baltic Sea. The fisheries of Flathead Lake, MT, have also experienced cascading effects from introductions of species, yet these effects have not been demonstrated for the Osprey population. The presence of detailed productivity and foraging data from before a major shift in the food web provides a unique opportunity to determine if these effects cascade to Ospreys.

Like many lakes and rivers in the world, introductions of non-native fishes and other biota have vastly altered the food web of Flathead Lake, MT (Table 1). By 1950, native species had begun to decline dramatically, and introduced kokanee salmon (*Oncorhynchus nerka*) had become the dominant pelagic fish. Managers also introduced the opossum shrimp (*Mysis relicta*), a pelagic amphipod that is a nearctic native with lake

Table 1. Fishes of the Flathead Basin, their origin, habitat and status (Table 1 in Stanford & Ellis, 2002)

Name	Species	Origin, Habitat ¹	Status ²
Bull trout	<i>Salvelinus confluentus</i>	N, a, f	A, D
Westslope cutthroat trout	<i>Parasalmo</i> ³ <i>clarkii lewsii</i>	N, a, f	A, D
RM whitefish	<i>Prosopium williamsoni</i>	N, a, f	A, S
Pigmy whitefish	<i>Prosopium colteri</i>	N, a	R, S
Largescale sucker	<i>Catostomus macrocheilus</i>	N, l	C, S
Longnose sucker	<i>Catostomus catostomus</i>	N, a, f	A, S
Northern pikeminnow	<i>Ptychocheilus oregonensis</i>	N, l, f	A, S
Peamouth minnow	<i>Mylocheilus caurinus</i>	N, l	C, S
Redside shiner	<i>Richardsonius balteatus</i>	N, l	A, S
Longnose dace	<i>Rhinichthys caractae</i>	N, f _{LR}	C, S
Slimy sculpin	<i>Cottus cognatus</i>	N, l, f	A, S
Shorthead sculpin	<i>Cottus confusus</i>	N, l, f	A, S
Lake whitefish	<i>Coregonus clupeaformis</i>	I-1890, a	C, E
Arctic grayling	<i>Thymallus arcticus</i>	I-1960s, a	R ⁴ , S
Kokanee salmon	<i>Oncorhynchus nerka</i>	I-1916, a	R, D
Yellowstone cutthroat trout	<i>Parasalmo</i> ³ <i>clarkii bouvieri</i>	I-1910s, a	R ⁴ , S
Lake trout	<i>Salvelinus namaychusch</i>	I-1905, l	A, E
Brook trout	<i>Salvelinus fontinalis</i>	I-1913, l, f	A, E
Rainbow trout	<i>Parasalmo mykiss</i>	I-1914, f	C, S
Golden trout	<i>Parasalmo aquabonita</i>	I-1960s, a	R ⁴ , S
Brown trout	<i>Salmo trutta</i>	I-1910s, f _{LR}	C, E
Yellow perch	<i>Perca flavescens</i>	I-1910, l	A, S
Northern pike	<i>Esox lucius</i>	I-1960s, l, f	R ⁵ , E
Pumpkinseed sunfish	<i>Lepomis gibbosus</i>	I-1910, l	C, S
Bluegill sunfish	<i>Lepomis macrochirus</i>	I-?, l	R ⁴ , ?
Black bullhead	<i>Amieurus melas</i>	I-1910, l	C, S
Yellow bullhead	<i>Amieurus natalis</i>	I-?, l	R, ?
Largemouth bass	<i>Micropterus dolomieu</i>	I-1898, l	R, S
Smallmouth bass	<i>Micropterus salmoides</i>	I-1960s, f _{LR}	C, E
Central mudminnow	<i>Umbra limi</i>	I-1990s, l	R, ?

¹Native (N) or Non-native (I) populations in Basin lakes (l) or rivers and streams (f), sometimes with adfluvial (a) life cycle (adults in lakes, spawn in tributary streams); f_{LR} are restricted to the Lower Flathead River downstream of the cataract where Kerr Dam was built in 1935.

²Distributed throughout the Basin (A), common (C) or restricted (R); population size stable (S), declining (D) or expanding (E). Bull trout are listed (L) under the Federal Endangered Species Act. Status based on State and Tribal census programs (unpublished data).

³We put the noble trouts in the genus *Parasalmo* after (Pavlov et al., 2001).

⁴Introduced adfluvial population in a few small lakes in the Basin.

⁵Restricted to: the littoral zone of Flathead Lake where it is rarely caught; a few small, shallow lakes in the Kalispell Valley; and, the Lower River and in the sloughs and oxbows immediately upstream of Flathead Lake.

trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*) in deep oligotrophic lakes. This crustacean was captured in Waterton Lake, where it is native, and released into Ashley, Swan, and Whitefish Lakes, which are upstream of Flathead Lake. The shrimp moved downstream and were first documented in Flathead Lake in 1981. Numbers increased exponentially through 1986 peaking at 180/m². The population then began to decline as the lake trout and lake whitefish fisheries expanded as a consequence of the sudden presence of their native deep water forage species (Spencer et al., 1991). Since 1990 the *Mysis* population has fluctuated around 40/m², apparently in relation to lake trout and lake whitefish recruitment (Deleray and Stanford, unpublished data).

Mysis shrimp are strong interactors in the food web. Historically, kokanee salmon and native trout had fed during daylight hours on large zooplankton. The shrimp out-competed these fish for their prey, because the shrimp fed at night and migrated to the bottom of the lake during the day. Lake trout and lake whitefish took advantage of this new deep-water food source, increased dramatically, and induced top-down control on the shrimp, which led to the decline and relative stabilization of the shrimp population. Subsequently, in Flathead Lake, westslope cutthroat (*Parasalmo clarkii lewisii*) and bull trout (*Salvelinus confluentus*) have nearly disappeared, and the last kokanee salmon was caught in 1987. Up to 118,000 kokanee had spawned each year in MacDonald Creek in Glacier National Park between 1975 and 1985. Only 50 kokanee spawned in MacDonald Creek in 1989. The fish biomass in the lake is now dominated by deep-water benthic-feeding fish species (i.e. lake whitefish and lake trout; lake whitefish comprise up to 80% of the fish biomass), as opposed to shallow water pelagic species (Spencer et. al 1991).

These studies also showed the cascading or strong interactive effects of species introductions on food web structure. The spawning kokanee salmon had been a major food source for migrating bald eagles, grizzly bears, river otters, mink, and even some white-tailed deer, along MacDonald Creek in Glacier National Park. Hundreds of Bald Eagles timed their migration to coincide with this massive spawning run. Since the loss of the kokanee from Flathead Lake, most of the eagles have shifted their migration paths to other locations (Spencer et al. 1991).

The effects of *Mysis* introduction influence human activities as well. Flathead Lake has long been used for tribal sustenance (the southern half of the lake is on the Flathead Indian Reservation), and has been popular for recreational anglers. Since the change in the food web, most anglers now aim for lake whitefish and trophy size lake trout, instead of native trout or kokanee salmon (Evarts, 1998). Furthermore, since the large lake trout are the top predatory fish in the lake, and have an additional trophic level below them (the *Mysis*), there is evidence of bioaccumulation of methylmercury (Hg) and polychlorinated biphenyls (PCBs) in the largest fish (Deleray et al., 1999; Stafford et al. 2001). This led Deleray et al. (1999) to suggest consumption limits of large lake trout, especially for children and pregnant women.

While the cascading effects on humans and migrating Bald Eagles have been documented, there has been limited evidence for similar effects on the main non-human piscivorian at Flathead Lake – Osprey. Since Osprey can only catch fish in the top one meter of the water column, a reasonable hypothesis is that the shift in fish-biomass to deeper water should have negatively affected Osprey foraging success, and thus lowered Osprey productivity.

In the 1960's, prior to the *Mysis* introduction, D. S. MacCarter and D. L. MacCarter gathered detailed population and diet data for the Osprey population at Flathead Lake (MacCarter, 1972a; MacCarter, 1972b; MacCarter & MacCarter, 1979). The unique availability of detailed diet and nesting studies prior to the food web shift make studying this Osprey population particularly useful in understanding cascading effects of species introduction in complex food webs of large lakes.

During the DDT era, the Flathead Lake Osprey population had been limited by low hatchability from bioaccumulation of DDT (MacCarter, 1972a). Since DDT was banned, MacCarter and MacCarter (1979), Klaver et al. (1982), and Mace et al. (1987) have studied the productivity of the Flathead Lake Osprey population. In that time, the number of productive nests dramatically increased, from less than 20 in the 1970's, to 67 in 2001. This population increase raises questions about how the Osprey population has adapted to the change in the food web after the removal of DDT from the system.

The availability of detailed data on the Osprey population from before the *Mysis* introduction (MacCarter, 1972a; MacCarter, 1972b; MacCarter & MacCarter, 1979) allows for pre and post-*Mysis* comparisons. The first objective of this study was to investigate correlative changes between the aquatic food web and the size of the Osprey population. Considering the shift in fish biomass from pelagic to deep-water species, a reasonable hypothesis would be that the Osprey population has less forage, and should therefore decline. However, the population has been concurrently released from the constraints imposed by DDT, and thus may have stabilized or increased. The second objective was to determine how the Ospreys have adjusted their diet to the new aquatic food web by comparing their 2001-02 diet to their diet in 1969-70. Since Ospreys are

usually non-selective foragers, any changes in their diet should reflect the changes in the fish community.

Chapter 2: Long-term Osprey (*Pandion haliaetus*) Population Dynamics in Relation to Food Web Change at Flathead Lake, MT.

Since European colonization of North America, Osprey (*Pandion haliaetus*) population dynamics have been influenced by anthropogenic disturbances. Ospreys were originally considered pests and competitors for fish. Deliberate extermination campaigns reduced populations worldwide (Poole, 1989). Even as late as the 1960's, shootings caused most mortality in a New Jersey Osprey population (Henny & Wight, 1969).

The single factor that resulted in perhaps the greatest loss of Osprey numbers, and many local extirpations, was the use of DDT as an agricultural pesticide. Due to bioaccumulation (increasing concentration with successive trophic level) concentration of contaminants may be high in apex predators. For birds at the top of the food web, most notably Bald Eagles (*Haliaeetus leucocephalus*) and Ospreys, DDT contamination was clearly shown to cause decreased shell thickness and increased occurrence of crushed and addled eggs (Poole, 1989; Ames & Mersereau, 1964). MacCarter (1972a) suggested that a low hatching rate, because of DDT, was the limiting factor in the Flathead Lake, MT, Osprey population. After DDT was banned continent-wide in the mid-1970's, many Osprey populations began recovering quickly (e.g. Henny et al. 1977; MacCarter & MacCarter, 1979), with annual increases of 6-15 % across the continent (Ewins, 1997).

The widespread population increases can also be attributed to legislative changes protecting Ospreys and Osprey habitat, and the increased availability and use of artificial structures for nests (Ewins, 1997; Poole, 1989). Ospreys are considered icons of conservation due to their cosmopolitan nature and quick recovery from DDT. They may

work as umbrella species for protecting entire aquatic ecosystems, as well as indicator species for food web, habitat, or chemical disturbances.

At Flathead Lake, MT, the increase in the Osprey population after the ban of DDT was described in a detailed study of Osprey ecology and productivity (MacCarter & MacCarter, 1979). Since then, however, the aquatic food web in Flathead Lake has changed dramatically. Prior to the mid-1980's, Flathead Lake was largely dominated by either native (westslope cutthroat trout, *Parasalmo clarkia lewisii*), or non-native (kokanee salmon, *Oncorhynchus nerka*), pelagic fish. The introduction of the opossum shrimp (*Mysis relicta*), a pelagic amphipod that is a nearctic native in deep oligotrophic lakes, resulted in significant increases in introduced lake trout (*Salvelinus namaychusch*) and lake whitefish (*Coregonus clupeaformis*). These two deep-water species, which are native predators of *Mysis*, now dominate the food web in Flathead Lake (Spencer et al., 1991; Stanford & Ellis, 2002). Since Ospreys are usually non-selective foragers (e.g. Dunstan, 1974), using fish species in similar proportions to their availability, the changes in the aquatic food web should have affected the Ospreys' diet, and possibly their productivity.

Previous detailed studies on the foraging and productivity of Ospreys at Flathead Lake (MacCarter, 1972a; MacCarter, 1972b; MacCarter & MacCarter, 1979) provide a unique opportunity to observe the results of this large-scale experiment. No other study has been able to compare Osprey foraging and nesting behavior over 30 years in one location, including a major change in the prey base.

The first objective of this study was to examine correlations between changes in the food web and changes in the Osprey population by comparing nest productivity,

numbers of fledglings, and number of active nests to pre-*Mysis* figures (MacCarter, 1972a; MacCarter and MacCarter 1979). Most studies of introduced species find disruption of the food web and declines in native species (Mooney & Hobbs, 2000). Since the dominant fish species are benthic, and pelagic fish species (kokanee salmon and cutthroat trout) have nearly disappeared, I hypothesized that the Osprey population is food limited, which would result in a decrease in nest and fledgling numbers since the *Mysis* introduction. However, any changes in the Osprey population in that time may also be attributed to the removal of DDT.

My second objective was to make temporal comparisons in foraging behavior since the *Mysis* introduction. I hypothesized that the shift in the aquatic community has changed how the Ospreys forage, and that their diet would reflect the changes in the fish community. Thus, I expected to find a similar percentage of largescale suckers, more lake whitefish, northern pikeminnow, and lake trout, and fewer cutthroat trout in the Osprey population's diet than MacCarter (1972b).

Study Area

The study area was the same as MacCarter (1972a), MacCarter (1972b), and MacCarter & MacCarter (1979, Figure 1) to ensure comparative data. It included an area north of the lake that is bounded by U.S. Highway 93 in the west, the Mission Mountains in the east, and continues to about seven km north of the lake. This area contains the upper Flathead River before it empties into Flathead Lake near Bigfork, MT, and the many sloughs and oxbows around the river, as well as the Swan River, from Flathead Lake to the dam east of Bigfork. The study area also includes Flathead Lake, which is about 28 miles long and 14 miles wide (153 miles of shoreline, surface area 482 km²,

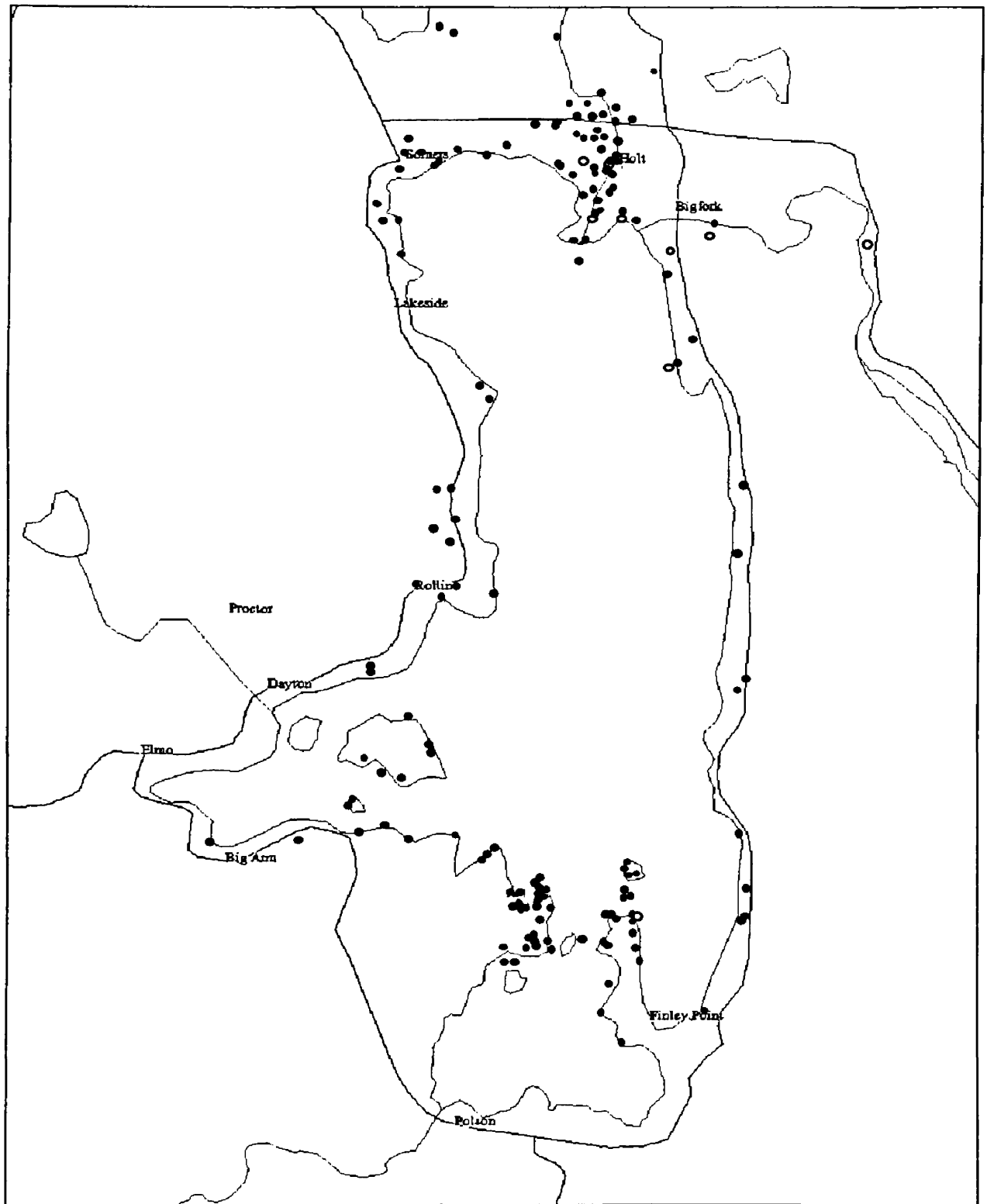


Figure 1: Osprey study area at Flathead Lake, MT. Pink = nests from 1967-70 (D.S. MacCarter, 1972); black = unproductive nests in 2001-02; red = productive nests in 2001 only; yellow = productive nests in 2002 only; orange = productive nests in both 2001 and 2002.

mean depth 52 m), down to Kerr Dam near Polson, MT, and all land visible from a boat on the water or from the roads that encircle the lake.

Methods:

All nests were located from the ground or by boat and canoe. I initially classified nests into three groups as defined by Postupalsky (1972): occupied, active, and successful. Due to weather and other logistics, not all nests could be checked immediately after nesting began, so some occupied nests may have been abandoned before the first check. I also did not climb any nest structures; therefore I could not confirm that a nest was active until nestlings could be spotted from the ground. To eliminate the chance that an active (i.e. containing young) nest that lost its young was classified as an occupied nest (adults present, but no eggs or young), I classified all nests as either productive (fledging at least one young) or not productive.

For each nest, I recorded nesting structure (e.g. telephone pole, dead conifer), number of fledglings, and coordinates. Nest coordinates were determined on a universal transverse mercator (UTM) grid by geographic positioning systems (GPS).

All observations were made in July and early August of 2001 and 2002. Each nest was visited for a minimum of 15 minutes, at least once every two weeks, to confirm the presence of adults and nestlings, and to collect prey remains from beneath the nest and nearby feeding perches. Additionally, I, or teams of trained volunteers, made longer (three to four hour) observations on selected nests with one, two, or three nestlings, during all daylight hours. This was intended to provide a detailed account of species and size of fish caught. Nests were not randomly selected for these observations due to constraints to property access, and feasibility and safety of observation posts. I also made

observations of potential foraging areas. The species of fish delivered to the nest or pulled from the water was determined by sight through binoculars and spotting scopes. Additionally, bones and scales that were collected from below accessible nests and feeding perches during the biweekly observations were compared to reference collections, which were made from fish caught in the lake.

Data analysis

I calculated productivity as the mean number of fledglings per productive nest.

MacCarter (1972b) collected fish remains from baskets placed beneath nests, and calculated dietary percentage as the number of bones from a given species divided by the total number of identifiable bones. Sampling prey remains in this way can underestimate the percentage of smaller fish presumably because smaller bones are more likely to be broken into pieces during feeding and less likely to be found on the ground (Carss & Godfrey, 1996). Additionally, since most of the prey remains found were individual bones or fins that were spread over a large area, I had to assume that each sample included different proportions of whole fish, with higher proportions skewed towards larger fish. For this reason I used an analysis technique that should help alleviate the above problems, but creates other biases.

I counted each successful collection of prey remains as a sample. Due to difficulty in determining the number of fish from individual bones in a given sample, I instead counted the number of samples that included at least one bone of a given species (sample-count). I calculated percent of diet as the sample-count for a given species divided by the total sample-count. For example, the sample-count for yellow perch was ten, with 78 total sample-counts; by this analysis strategy, yellow perch made up about

13% of the diet (Table 2). However, there may have been more than ten yellow perch in all of the samples, in which case this method would underestimate the importance of yellow perch. Likewise, a sample that actually contained one peamouth and many lake whitefish would be listed as containing only one of each species. After examining many samples that contained multiple fish, this method would underestimate the percentage for frequently captured fish, and overestimate the percentage for rarely captured fish, essentially rounding off the peaks. Therefore, any differences in percentage between species are likely conservative estimates. However, since the bones rarely last for more than 24 hours on the ground before being taken by other animals (Poole, 1989), the chance that a sample contained more than one-day's worth of fish was small, and, therefore, the just-mentioned bias would be limited. For the purposes of this paper, this strategy should yield comparable data to MacCarter (1972b) since I am examining general trends, rather than exact changes.

All large bones were identified to species, but most in-flight observations were unidentifiable to species. Since at least four potential prey species were salmonids, which all have similar body shapes, it was extremely difficult to distinguish species carried by a flying Osprey. The counts from fish remains differed significantly from observations of prey delivery (Figure 2; $G=18.2$, $df=5$, $p=0.003$). For this reason, all comparisons of diet between studies use percentages of prey remains, rather than in-flight observations in MacCarter (1972b) and Ring and Stanford (1990).

To estimate trends in prey species availability, I examined differences between pre- (1981, 1983) and post-*Mysis* (1997, 1998) floating gill net data (Deleray et. al, 1999). Sinking gill net data better demonstrate the changes in the fish community as a

whole, but do not reflect the changes in the upper one-meter of the water column, which is the only depth available to Osprey. I used G-tests to compare Osprey diet of this study to prey remains in MacCarter (1972b). Productivity and number of nests and fledglings were only compared to MacCarter (1972a), MacCarter & MacCarter (1979) and data for 1979 in Klaver et al. (1982), which included the same study area. Unless otherwise noted, all results are given as mean \pm SD.

Results

A total of approximately 400 hours were spent in both short and long observations, in July and August of 2001 and 2002, by me, two other researchers (C. Blem, L. Blem), and 23 trained volunteers. In 2002 I found only one nest that had likely been in existence in 2001, but had not been recorded. Therefore, I am confident that this study found all of the nests in this study area (Figure 1). Nest coordinates and individual fledgling numbers are given in Appendix 1.

Nest Numbers and Productivity

Productive nests increased from the pre-*Mysis* high of 20 in 1979 (Klaver et al., 1982), to 67 in 2001. Number of fledglings increased from 58 to 131 in that same time. There was a dramatic decline between 2001 and 2002 in the number of successful nests (from 67 to 32), and number of fledglings (from 131 to 65; Figure 3). Regardless of this decline, it is obvious that there are now more successful nests and more fledglings than 20 years ago. Productivity (number of fledglings per productive nest) was slightly higher in 2001 and 2002 (2.00 ± 0.05) than 1967-1970 (1.85 ± 0.17), but lower since 1977 and 1979 (2.53 ± 0.19 ; Figure 4; MacCarter & MacCarter, 1979; Klaver et al., 1982).

Table 2: Fish remains found beneath Osprey nests around Flathead Lake, MT, in 2001 and 2002. Each sample was a collection of all remains found under the nest, collected during biweekly visits. Numbers in species columns represent the number of samples containing that species.

Nest	# samples	LSS [†]	YP [†]	NPM [†]	LT [†]	LWF [†]	PM [†]	tot
UR4	11	8	4	4	8	4	3	31
UR21	2	1	0	2	1	1	1	6
L59	2	2	0	0	1	1	1	5
UR7	2	1	0	0	0	1	0	2
UR12	1	0	1	0	0	0	0	1
UR11	1	1	0	0	0	1	0	2
L11	2	1	0	1	1	0	0	3
UR23	1	0	0	1	1	0	0	2
L64	1	0	0	0	0	1	0	1
L4	2	1	2	0	1	2	0	6
L21	1	1	0	0	0	1	0	2
L46	3	1	1	2	2	1	1	8
L45	4	0	1	0	0	2	1	4
L29	1	1	0	0	0	0	0	1
TP2	1	0	1	1	1	0	0	3
Total	35	18	10	11	16	15	7	77
% of identified fish		23.4	13.0	14.3	20.8	19.5	9.1	100.0

LSS=Largescale sucker; YP=Yellow perch; NPM=Northern pikeminnow;
 LT=Lake trout; LWF=Lake whitefish; PM=Peamouth

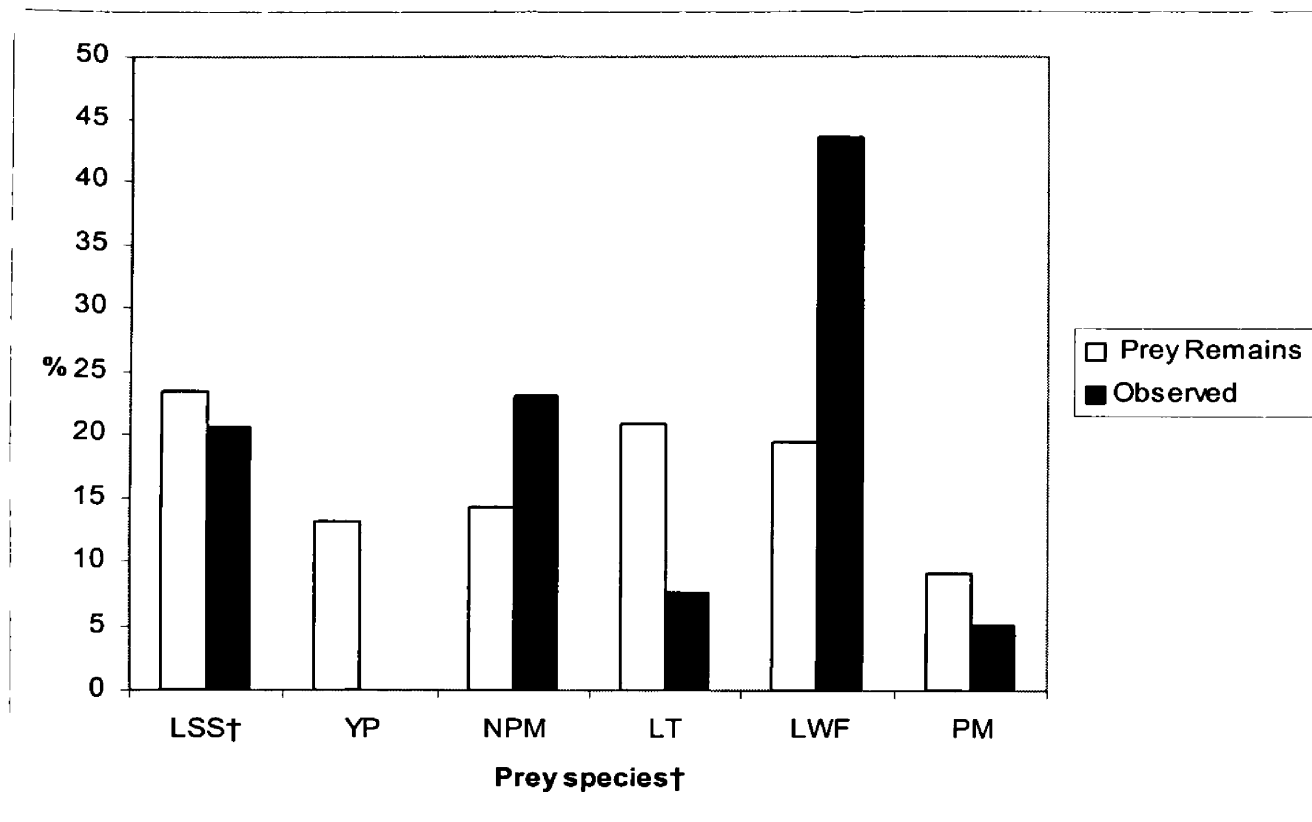


Figure 2: Species presence in samples of remains compared to percent of times the same species was clearly observed being carried by Ospreys at Flathead Lake, MT, in 2001 and 2002. Differences between remains and observed were significant ($G=18.2$, $df=5$, $p=0.003$).

†LSS=Largescale sucker; YP=Yellow perch; NPM=Northern pikeminnow; LT=Lake trout; LWF=Lake whitefish; PM=Peamouth

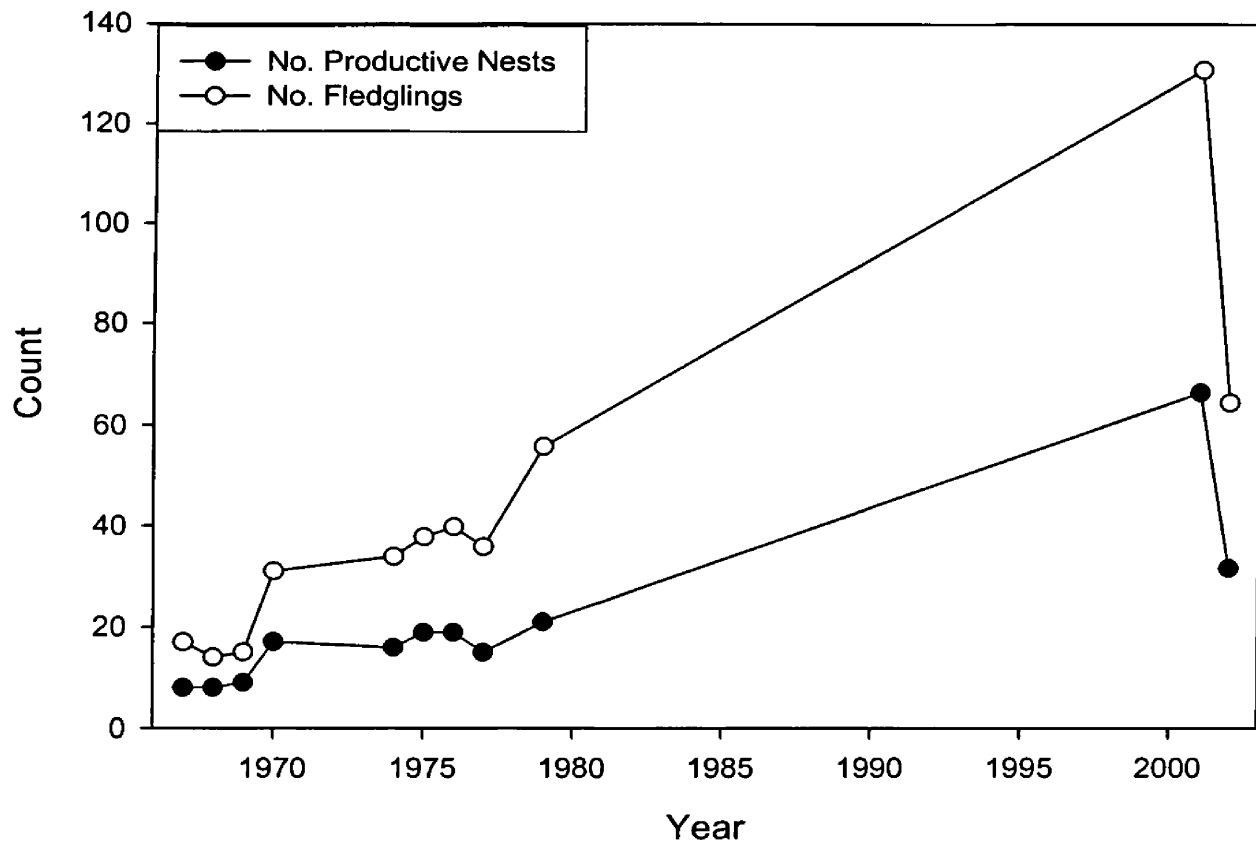


Figure 3: Number of productive nests and fledglings over 35 years at Flathead Lake (1978 and earlier data from MacCarter & MacCarter, 1979; 1979 data from Klaver et al, 1982; 2001 and 2002 data from this study).

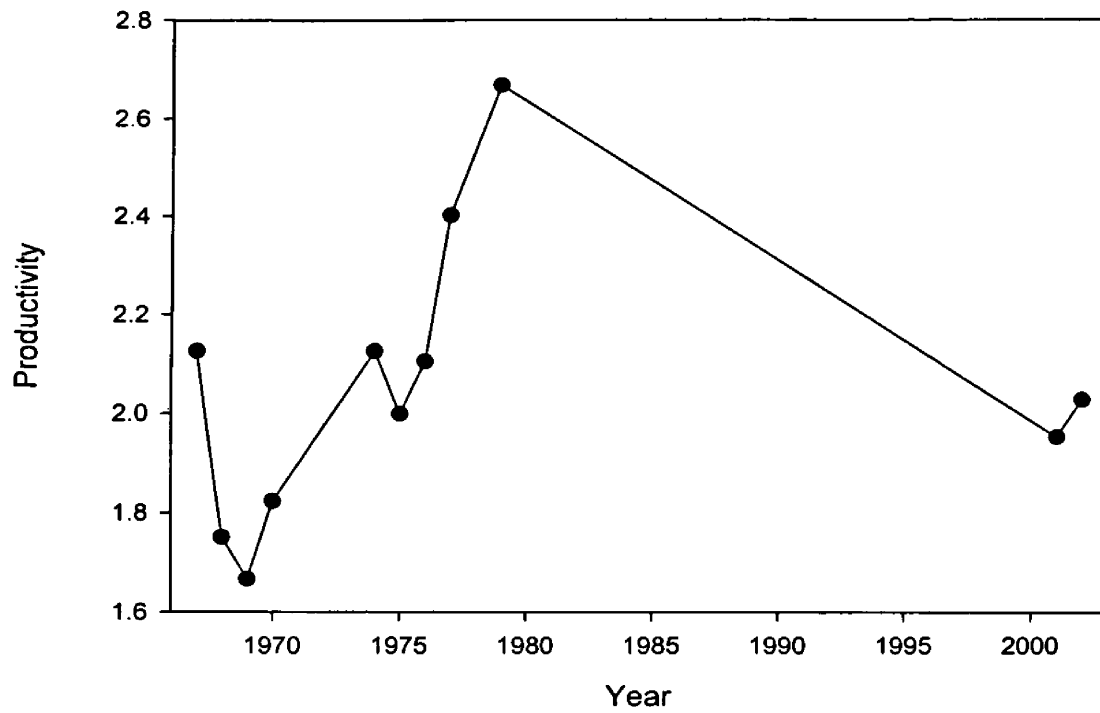


Figure 4: Productivity (calculated as mean number of fledglings per productive nest) over 35 year at Flathead Lake (1978 and earlier data from MacCarter & MacCarter, 1979; 1979 data from Klaver et al, 1982; 2001 and 2002 data from this study).

Temporal diet comparison

The prey remains were significantly different from prey remains found by MacCarter (1972b, $G=25.1$, $df=5$, $p=0.0001$; Figure 5). I found no evidence that Ospreys were feeding on westslope cutthroat trout, black bullhead, or sunfish, all of which were found by MacCarter (1972b). There was no obvious change in percentage of lake whitefish (22.5 to 19.5 %), peamouth (2.9 to 9.1%), or yellow perch (2.9% to 13.0%). I found significant levels of both lake trout (20.8 %) and northern pikeminnow (14.3 %), neither of which was present in the Ospreys' diet in 1967-1970. There was also an obvious decrease in the percentage of largescale suckers (48.4% to 23.4%; Figure 5). Both pre- and post-*Mysis*, relative to floating gill net samples, the Osprey diet contained higher percentages of largescale suckers and lake whitefish, and lower percentages of peamouth and westslope cutthroat trout. In the current study, the Osprey diet also contained a higher percentage of lake trout, and a lower percentage of northern pikeminnow, compared to the gill net data (Figure 5).

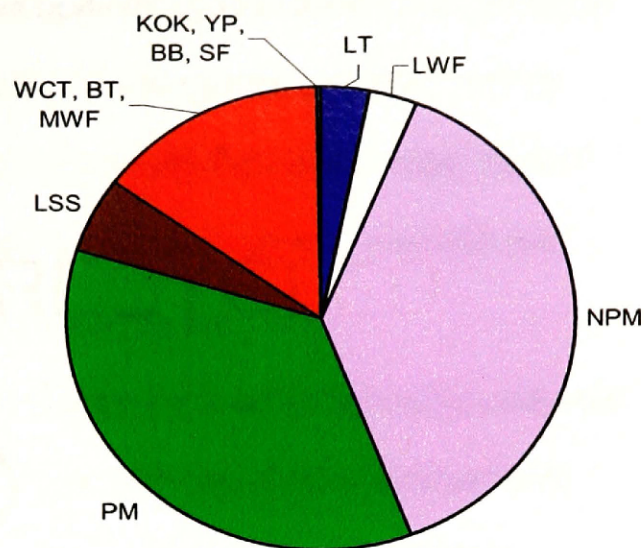
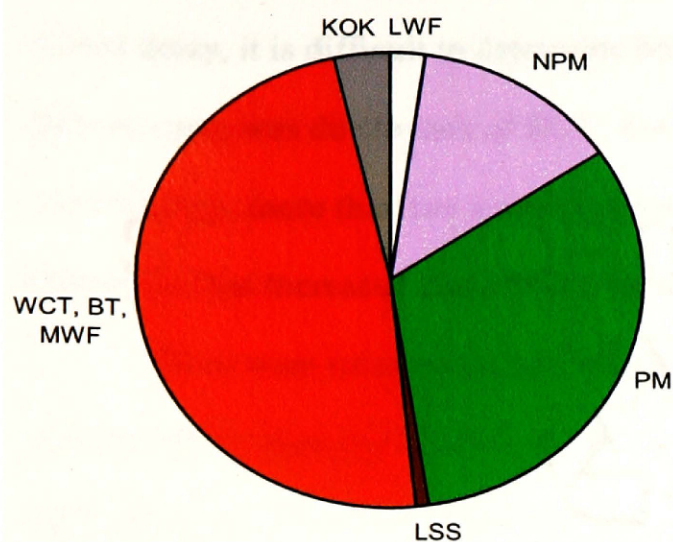
Discussion

Nest Numbers and Productivity

By interpreting numbers of nests and fledglings, it is clear that the Osprey population has increased. Part of this increase is likely due to an increase in hatching success after the ban of DDT. MacCarter (1972a) found negative correlations between DDT contamination in prey items, shell thickness, and reproductive success in the Ospreys at Flathead Lake, where DDT concentrations were 40% higher in Osprey eggs than in samples of fish. Since Ospreys do not return to their breeding grounds until two years after they hatch, and do not breed until one or two years after that (Poole, 1989),

Pre-Mysis Gill Net (1981, 1983)

Post-Mysis Gill Net (1997-98)



Osprey Diet (1969-70)

Osprey Diet (2001-02)

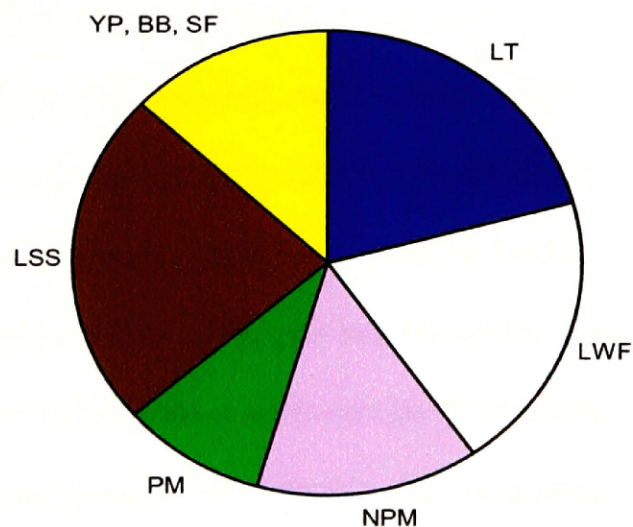
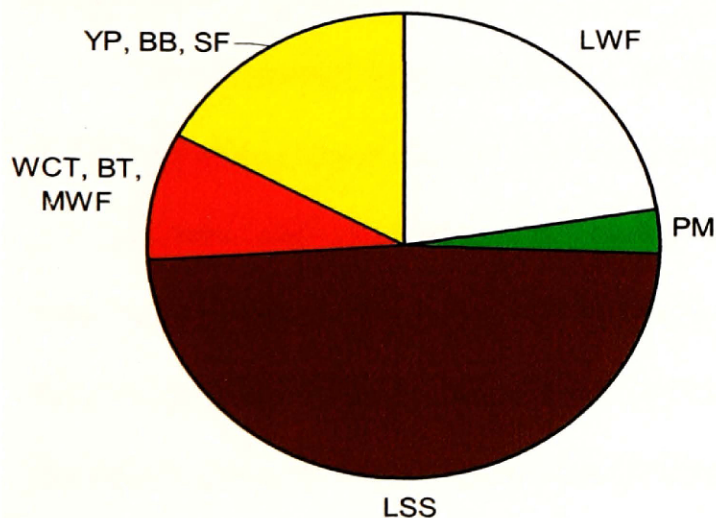


Figure 5: Percent composition of gill net surveys (Deleray et al., 1999) and Osprey diet. Data from 1969-70 are from prey remains below nests (MacCarter, 1972). Data from 2001-02 are from prey remains below nests (this study). Prey species abbreviations as follows: BB=black bullhead, BT=bull trout, KOK=kokanee salmon, LSS=largscale sucker, LT=lake trout, LWF=lake whitefish, MWF=mountain white fish, NPM=northern pikeminnow, PM=peamouth, SF=sunfish, WCT=westslope cutthroat trout, YP=yellow perch.

recruitment to the breeding population is delayed. Therefore, any increase in hatching success would not be seen as an increase in active nests for at least three years. Because of this delay, it is difficult to determine how much of the population increase over the past 30 years was due to lack of DDT, the change in the food web, or any other factors. Nevertheless, more than ten years after the change in the food web it is clear that the population has increased since before the introduction of *Mysis*.

There were more nests, more fledglings, and higher productivity in this study than in 1967-1970. However, when compared to 1977 and 1979 (MacCarter & MacCarter, 1979; Klaver et al. 1982), productivity was lower, even though nest and fledgling numbers were higher. The same inverse relationship between productivity and numbers of nests and fledglings can be seen in 2001 and 2002 (Figure 3, 4).

Many studies have used Henny & Wight's (1969) calculations of 0.95 to 1.30 fledglings per *occupied* nest to determine Osprey population sustainability. Productivity per occupied, active, and/or productive nest is reported in virtually every Osprey study, thus I report it here. However, the comparison between this study and previous data, and the comparison between years of this study, are excellent case studies in how misleading productivity can be as a measure of population demographics for Osprey. By comparing only productivity, I would conclude that the Flathead Lake Osprey population was healthier in 1977-79 than in 2001-02, and healthier in 2002 than in 2001. I would also conclude that productivity was as low in 2001-2002 as it was while DDT was still in use. However, looking at either the number of successful nests or number fledglings would lead to opposing conclusions.

Per-nest productivity is an index of nestling survival, as calculated here, or egg survival (if calculated per *active* nest), to fledging, after which there is little or no demographic data in most studies. Post-fledgling survival rates may greatly vary between populations and times. For example, Henny and Wight (1969) found that most mortality in a New Jersey population was due to shootings, which is likely no longer the case, and may never have been the case in Montana. Mean productivity can also be misleading as populations recover. Lohmus (2001) found that during recolonization of an area, the highest quality nests were occupied first, which increased the mean productivity. As the population grew, lower quality nests were occupied, lowering the mean productivity, even though the number of successful nests and fledglings had increased. Therefore, nest productivity has little usefulness as an index of population success when comparing populations, whether between locations or decades.

Temporal diet comparison

The three species of fish that increased in the lake the most after the *Mysis* introduction, according to the floating gill netting data, were the lake whitefish, lake trout, and northern pikeminnow. Most of the increase in lake whitefish and lake trout can be seen in sinking rather than the floating gill net data (Deleray et al., 1999), suggesting that most of the new fish are out of reach for Osprey. However, northern pikeminnow feed in shallower water on fish or insects, so they should be more available to Ospreys than lake trout and lake whitefish.

Lake whitefish did not make up any more of the Osprey diet in 2002 than 1969-70, even though they constitute over 80% of the fish caught in sinking gill nets (Deleray, 1999). Considering that lake whitefish tend to stay in deep water, it is somewhat

mysterious that the Osprey caught as many lake whitefish as they did in both studies, but personal observations lead to one hypothesis. On five occasions I observed Ospreys picking up dead lake whitefish off the surface of the water, without diving. These fish may have died after having been reeled up from deep water, causing their swim bladder to rupture. Dunstan (1974) observed at least three occasions of Osprey picking dead yellow perch or other dead fish left by fishermen off the surface of the water. Ewins (1994) described two Ospreys picking up dead black crappie near ice fishing holes on Lake Huron. Bent (1937) also documented Ospreys scavenging fish, but these appear to be the only documented cases of such behavior.

The big changes in Osprey diet were percentages of lake trout and northern pikeminnow. They ranked second and fourth in 2002, but MacCarter (1972b) found neither species. Lake trout tend to stay in the deep water, but may make occasional foraging trips to the surface. They are also fished for heavily (Evarts, 1998), and some may suffer the same fate as the lake whitefish I saw picked off the surface. Northern pikeminnow numbers more than doubled in the floating gill net surveys, and went from zero to 14% of the Osprey diet.

MacCarter (1972b) found black bullhead, sunfish, and westslope cutthroat trout in the diet of the Ospreys 30 years ago. I found no evidence that the Ospreys used these fish in 2001-02. Gill netting did not record presence of black bullhead or sunfish so I cannot say if the lack of these species in the Ospreys' diet is due to a decrease in their populations. Black bullhead and sunfish were probably never common in Flathead Lake. The Ospreys may have caught them in nearby ponds and oxbows, which experienced total winter fish kills, due to low water levels and full depth freezing, in early 2001 (Jack

Stanford, pers. comm.). Westslope cutthroat trout are a species of regional concern due to significant population declines in lakes and rivers from habitat loss and competition with non-native rainbow trout (Allendorf & Leary, 1988). In Flathead Lake, cutthroat trout significantly declined after the establishment of *Mysis* (Deleray et al., 1999). Likewise, they declined in the Ospreys' diet from 8.8% in 1969-1970, to zero in 2001-2002.

In the current study and MacCarter (1972b), largescale suckers made up a much greater percentage of the Osprey diet than were available, according to the gill net samples. However, MacCarter (1972b) found that the Ospreys were foraging for suckers in the rivers, for which there is no gill net data. The percentage of suckers in the diet declined between 1969-70 and this study. I suggest two hypotheses for why suckers made up less of the Osprey diet in 2001-02. The Ospreys are no longer fishing in the rivers as much as MacCarter (1972b) observed, and instead the Ospreys have selected to forage in the main body of the lake, perhaps finding new species of fish (e.g. lake trout and northern pikeminnow). Alternatively, there may have been a decline in the largescale sucker population related to the changes in the food web. Such a decline could have been caused by increased predation by lake trout, which are very abundant in the rivers today, and very food limited. Such a decrease in suckers would not show up in gill netting data, since all the gill nets were placed in the main body of the lake. If this was the case, the Ospreys may have been forced, rather than selected, to forage in the main body of the lake.

The fish species that saw the most severe declines after the introduction of *Mysis* was the kokanee salmon. It went from being the dominant species at hundreds of

thousands of individuals to zero in Flathead Lake (Spencer et al, 1991). Even at such high pre-*Mysis* numbers, kokanee did not show up in either the gill-netting or Osprey data. Kokanee are highly visual, schooling, pelagic foragers. The high agility and visual acuity in similarly foraging cutthroat trout reduced Osprey dive success from 70% on benthic-feeding fish to 30% (Swenson, 1979). The kokanees' visual acuity probably helped them avoid both the gill nets and soaring Ospreys, explaining the absence in either data set of the most numerous fish in the lake.

Collecting fish remains from below Osprey nests is common practice in dietary studies (e.g. MacCarter, 1972b; Dunstan, 1974; Swenson, 1978; Carss & Godfrey, 1996). This technique is very accurate, but it can underestimate percentages of fish smaller than 25 cm in the diet. Compared to the only other non-invasive technique of observing fish as they are carried to the nest, which gives a good estimate of size, examining fish remains should give a better estimate of prey species ratios if the possible prey species have similar body shapes (Carss & Godfrey, 1996).

In summary, in 2001-02 the Ospreys ate less sunfish, black bullhead, westslope cutthroat trout, and largescale suckers than in 1969-70. The decline in largescale suckers in the diet is compensated for by the increased use of lake trout and northern pikeminnow, both of which increased in the lake after the *Mysis* introduction. From these data, it is apparent that the change in the fish community did affect the foraging behavior of the Ospreys, but not exactly in the way that I had predicted. Compared to MacCarter (1972b), the Ospreys foraged less in the rivers – possibly because there are fewer largescale suckers – and more in the lake fishing for northern pikeminnow and lake trout.

Overall, they adjusted to the fish changes by using fish that are now more available, supporting my hypothesis.

Ideas for Further Study

While the foraging data obtained from collecting prey remains below nests is standard practice, it could be improved in the continuation of this study. MacCarter (1972b) erected wire baskets below nests and feeding perches to collect remains, and prevent their being removed and/or eaten by other animals. This is one possibility, but it may be just as effective to increase sampling frequency at each nest. This way, there would be less chance of losing prey remains to other animals. Additionally, increasing the sampling frequency would increase total sample size per year, and may allow comparison of prey selection within a season. Lake trout and lake whitefish can be found in shallower waters until establishment of the thermocline, which usually occurs in late June, about the time that I began collecting prey remains. Therefore I would expect to find more of these species in the Osprey diet early in the nesting season.

While adult Ospreys are extremely difficult to catch and handle, and many nests in this study area are not accessible, I would also suggest banding Ospreys in this population, including colored bands to identify individuals from a distance. Little or nothing is known for this population about migration strategies and locations, degree of regional and nest philopatry, or age structure. Favored foraging grounds could also be identified for individuals and correlated with percentages of species in the diet.

Osprey-Bald Eagle interactions present additional research opportunities. Bald Eagles also declined severely from hunting and pollution, but have recovered more

slowly than the Osprey. As the eagles increase in numbers, they have begun to displace some Osprey (Ogden, 1975; Ewins 1997). Eagles at Flathead Lake defend large areas around their nests (pers. obs). In one location (Bird Island), I found one active eagle nest as the only large bird nest in an area that had held multiple Osprey nests (MacCarter, 1972a). I have observed multiple occasions of aggressive behaviors between individuals of the two species, initiated by both species. I also found the wing of an adult Osprey beneath a Bald Eagle nest. Elsewhere, Bald Eagles have even been observed attacking an Osprey nestling to steal food (Flemming & Bancroft, 1990). However, in areas where food is not limiting, Osprey and Bald Eagles can nest near to each other, and do not interact aggressively (Dunstan, 1974; Ogden, 1975). Further spatial analysis is needed, comparing territorial buffers around Bald Eagle nests with behavioral observations of Osprey-Eagle interactions.

Conclusions

After DDT was banned and artificial nest structures were erected, the Osprey population at Flathead Lake grew. The introduction of *Mysis*, which dramatically changed the food web within the lake, apparently had little effect on Osprey success. The Ospreys adjusted to forage for the available species of prey while increasing their numbers, even though some of the new prey was mostly benthic and some natural nest sites had been lost. There was no evidence that the change in the food web negatively affected the Osprey, as it did migrating Bald Eagles (Spencer et al, 1990). In fact, the evidence suggests that this Osprey population is not food-limited at all, and may still be recovering from the detrimental effects of DDT.

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Literature Cited

- Allendorf, F. R., and R. Leary. 1988. Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout. *Conservation Biology* 2:170-184.
- Ames, P. L., and F. S. Mersereau. 1964. Some factors in the decline of the Osprey in Connecticut. *The Auk* 81: 173-185.
- Austin-Smith, P. J., and G. Rhodenizer. 1983. Ospreys, *Pandion haliaetus*, relocate nests from power poles to substitute sites. *Canadian Field-Naturalist* 97: 315-319.
- Bent, A. C. 1937. Life histories of North American birds of prey. Pt 2. U.S. National Museum Bulletin 195:352-379.
- Carss, D. N., and J. D. Godfrey. 1996. Accuracy of estimating the species and sizes of Osprey prey: a test of methods. *Journal of Raptor Research* 30: 57-61.
- Chubbs, T. E., and P. G. Trimper. 1998. The diet of nesting Ospreys, *Pandion haliaetus*, in Labrador. *The Canadian Field Naturalist* 112:502-505.
- Deleray, M., L. Knotek, S. Rumsey, and T. Weaver. 1999. Flathead Lake and River system fisheries status report. Montana Fish, Wildlife and Parks, Kalispell, MT.
- Dunstan, C. 1974. Feeding activities of Ospreys in Minnesota. *The Wilson Bulletin* 86: 74-76.
- Edwards, T. C. Jr. 1989. The ontogeny of diet selection in fledgling Ospreys. *Ecology* 70: 881-896.
- Evarts, L. 1998. A review of creel survey information on Flathead Lake and a perspective on lake trout 1962-1996. Confederated Salish and Kootenai Tribes, Pablo, Montana.

- Ewins, P. J. 1997. Osprey (*Pandion haliaetus*) populations in forested areas of North America: changes, their causes and management recommendations. *Journal of Raptor Research* 31: 138-150.
- Ewins, P. J., and E. Cousineau. 1994. Ospreys (*Pandion haliaetus*) scavenging fish on ice. *Journal of Raptor Research* 28:120.
- Flemming, S. P., and R. P. Bancroft. 1990. Bald Eagle attacks Osprey nestling. *Journal of Raptor Research* 24:26-27.
- Flemming, S. P., and P. C. Smith. 1990. Environmental influences on Osprey foraging in northeastern Nova Scotia. *Journal of Raptor Research* 24: 64-67.
- Greene, E. 1987. Individuals in an Osprey colony discriminate between high and low quality information. *Nature* 329:239-241.
- Grubb, T. C. 1977a. Why Ospreys hover. *The Wilson Bulletin* 89:149-150.
- Grubb, T. G. Jr. 1977b. Weather-dependent foraging in Ospreys. *Auk* 94:146-149.
- Hagan, J. M. 1986. Temporal patterns in pre-fledgling survival and brood reduction in an Osprey colony. *The Condor* 88:200-205.
- Henny, C. J., and H. M. Wight. 1969. An endangered Osprey population: estimates of mortality and production. *The Auk* 86:188-198.
- Henny, C. J., M. A. Byrd, J. A. Jacobs, P. D. McLain, M. R. Todd, and B. F. Halla. 1977. Mid-Atlantic coast Osprey population: present numbers, productivity, pollutant contamination, and status. *Journal of Wildlife Management* 41:254-265.
- Henny, C. J., J. A. Collins, and W. J. Deibert. 1978. Osprey distribution, abundance, and status in western North America: II. The Oregon population. *The Murrelet* 59:14-25.

- Klaver, R. W., J. M. Smith, J. J. Claar, B. L. Betts, and L. C. Peterson. 1982. Osprey surveys in the Flathead Valley, Montana, 1977-1980. *The Murrelet* 63:40-45.
- Lohmus, A. 2001. Habitat selection in a recovering Osprey *Pandion haliaetus* population. *Ibis* 143:651-657.
- MacCarter, D. L. 1972a. *Reproductive performance and population trends of Ospreys at Flathead Lake, Montana*. Masters thesis. Humbolt State University.
- MacCarter, D. S. 1972b. *Food habits of Ospreys at Flathead Lake, Montana*. Masters Thesis, Humbolt State University.
- MacCarter, D. L., and D. S. MacCarter. 1979. Ten-Year Nesting Status of Ospreys at Flathead Lake, Montana. *The Murrelet* 60: 42-49.
- Mace, R. D., D. Casey, and K. Dubois. 1987. *Effects of water level fluctuations on productivity and distributions of Ospreys and Bald Eagles in the northern Flathead valley*. Final Report, Montana Department of Fish, Wildlife, and Parks, Kalispell, MT.
- Mooney, H. A., and R. J. Hobbs. 2000. *Invasive Species in a Changing World*. Island Press, Washington, D.C. 457 pp.
- Moyle, P. B., H. W. Li, and B. A. Barton. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America. Pages 415-426 in R.G. Stroud, ed. *Fish Culture in Fisheries Management*. American Fisheries Society, Bethesda, MD.
- Ogden, J. C. 1975. Effects of Bald Eagle territoriality on nesting Ospreys. *Wilson Bulletin* 87: 496-505.

- Olenin, S., and E. Leppakoski. 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. *Hydrobiologia* 393:233-243.
- Poole, A. F. 1989. *Ospreys a Natural and Unnatural History*. Cambridge University Press, Cambridge, UK. 246 pp.
- Poole, A. F., R. O. Bierregaard, and M. S. Martell. 2002. Osprey (*Pandion haliaetus*). *In The Birds of North America*, No. 683 (A. Poole and F. Gill, eds.) The Birds of North America, Inc., Philadelphia, PA.
- Postupalsky, S. 1972. A critical review of problems in calculating osprey reproductive success. *In Transactions of the North American Osprey Research Conference*. John C. Ogden (ed.) U.S. Department of the Interior, National Park Service Transactions and Proceedings Number Two, 1977. pp. 1-12.
- Reese, J. G. 1977. Reproductive success of Ospreys in central Chesapeake Bay. *The Auk* 94: 202-221.
- Ring, S. and J. A. Stanford. 1990. Recent disturbance in the Flathead Lake (Montana) Ecosystem: How does the Osprey fare? *Proceedings of the Montana Academy of Science* 50:29-35.
- Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagle displacement; cascading interactions in the food web of a large aquatic ecosystem. *BioScience* 41:14-21.
- Stafford, C. P., B. Hansen, J. A. Stanford. 2001. Mercury in the food web of Flathead Lake, Montana, U.S.A. Open File Report #164-01. Flathead Lake Biological Station, The University of Montana, Polson, Montana. 29 pp.

- Stanford, J. A. and B. K. Ellis. 2002. Natural and cultural influences on ecosystems processes in the Flathead River Basin (Montana, British Columbia). Pp 269-284. In: Baron, J. S. (eds). *Rocky Mountain Futures: An Ecological Perspective*. Island Press, Covelo, California, USA. 325 pp.
- Stinson, C. H. 1978. The influence of environmental conditions on aspects of the time budgets of breeding Ospreys. *Oecologia* 36:127-139.
- Stinson, C. H., J. Lauthner, and R. T. Ray. 1987. The effect of weather conditions on the behavior of Ospreys in northwestern Washington. *Canadian Journal of Zoology* 65:2116-2118.
- Swenson, J. E. 1978. Prey and foraging behavior of Ospreys on Yellowstone Lake, Wyoming. *Journal of Wildlife Management* 42:87-90.
- Swenson, J. E. 1979. Factors affecting status and reproduction of Ospreys in Yellowstone National Park. *Journal of Wildlife Management* 43:595-601.
- Swenson, J. E. 1981. Osprey nest site characteristics in Yellowstone National Park. *Journal of Field Ornithology* 52:67-69.
- Vana-Miller S.L. 1987. *Habitat Suitability Index Models: Osprey*. U.S. Fish and Wildlife Service: Biological Report 82(10.154)
- Ward, P., and A. Zahavi. 1973. The importance of certain assemblages of birds as "information centres" for food finding. *Ibis* 115:517-534.

Appendix 1: Nest categories, numbers fledged, structures, and MTU coordinates.

*DC=Dead Conifers; L CW= Live Cottonwoods; LC=Live Conifers; PF/TP=Nesting Platforms/Telephone Pole Nesting Platforms; CT=Cell Phone Towers

ID #	colonial/solitary	No. fledged (2001)	No. fledged (2002)	Site*	MTUe	MTUn
L44	solitary	3	gone	DC	722482	5307038
UR19	colonial	3	3	DC	715090	5329300
UR7	colonial	3	3	TP	712324	5330855
L17	colonial	3	2	LC	714110	5296436
L41	solitary	3	2	PF	710400	5319000
UR21	colonial	3	2	TP	706432	5329688
UR6	colonial	3	2	TP	713210	5330600
L14	colonial	3	0	DC	715000	5296050
L51	solitary	3	0	DC	718089	5294580
L32	solitary	3	0	DC	708982	5304044
L53	solitary	3	0	LC	707253	5305808
L10	colonial	2	gone	DC	716995	5294792
L43	solitary	2	gone	DC	723375	5296253
L40	colonial	2	3	PF	706403	5326012
UR11	colonial	2	3	TP	711982	5334870
L46	solitary	2	3	TP	706651	5324534
L8	colonial	2	2	PF	717865	5294750
L37	colonial	2	2	PF	707615	5328630
UR4	colonial	2	2	TP	713541	5330447
UR29	colonial	2	2	TP	712800	5331950
UR23	solitary	2	2	TP	719170	5327200
UR13	solitary	2	2	TP	716043	5333731
L5	colonial	2	1	DC	719209	5294574
L34	solitary	2	1	DC	707355	5301970
UR9	colonial	2	1	TP	714135	5328890
UR3	colonial	2	1	TP	713945	5330510
L31	colonial	2	0	DC	714361	5293461
L13	colonial	2	0	DC	715027	5296591
L16	colonial	2	0	DC	714855	5297071
UR30	colonial	2	0	DC	706320	5329050
UR18	colonial	2	0	DC	714580	5329150
UR17	colonial	2	0	DC	714722	5331315
L20	solitary	2	0	DC	718269	5292882
L52	solitary	2	0	DC	714050	5295950
L3	solitary	2	0	DC	723506	5296466
L2	solitary	2	0	DC	723445	5297675
L33	solitary	2	0	DC	708530	5299045
L50	solitary	2	0	DC	709180	5312450
L22	solitary	2	0	DC	721583	5312616
L29	solitary	2	0	DC	721480	5315680
L23	solitary	2	0	DC	717484	5324721
L21	solitary	2	0	DC	705788	5325932
L26	colonial	2	0	L CW	714371	5327751
L19	colonial	2	0	PF	713859	5296566
L25	colonial	2	0	PF	714305	5327145

ID #	colonial/solitary	No. fledged (2001)	No. fledged (2002)	Site	MTUe	MTUn
L24	colonial	2	0	PF	715394	5327352
L38	colonial	2	0	PF	706223	5328290
L42	solitary	2	0	Tower	718800	5321962
UR20	colonial	2	0	TP	708450	5329400
UR2	colonial	2	0	TP	714320	5330580
UR10	colonial	2	0	TP	711514	5330876
UR22	colonial	2	0	TP	713770	5331466
UR15	colonial	2	0	TP	707200	5334850
L11	colonial	1	gone	DC	713961	5293433
L45	solitary	1	3	TP	705476	5326641
L4	solitary	1	2	DC	722305	5292063
L12	colonial	1	0	DC	715030	5294787
L6	colonial	1	0	DC	719031	5295238
L7	colonial	1	0	DC	718277	5295800
L15	colonial	1	0	DC	715050	5296880
L49	solitary	1	0	DC	705100	5298050
L1	solitary	1	0	DC	722905	5300084
L48	solitary	1	0	DC	710350	5310001
L54	solitary	1	0	DC	709100	5314200
L35	colonial	1	0	PF	713728	5327898
L36	colonial	1	0	PF	712686	5329095
UR1	colonial	1	0	TP	714900	5330434
UR5	colonial	0	gone	Barn	713150	5330200
L77	solitary	0	3	DC	717500	5325800
L55	solitary	0	3	LC	717400	5320600
L78	colonial	0	2	L CW	714200	5326900
L47	colonial	0	2	PF	715400	5327000
L60	solitary	0	2	Tower	719000	5326600
L28	colonial	0	2	TP	714630	5329350
UR41	colonial	0	2	TP	714630	5329350
UR39	colonial	0	2	TP	713600	5329400
L30	colonial	0	1	DC	719150	5296000
UR53	solitary	0	1	LC	727812	5326900
L9	colonial	0	0	DC	717865	5295940
L18	colonial	0	0	DC	714400	5295980
L58	colonial	0	0	DC	709700	5314300
L57	colonial	0	0	DC	711900	5309800
L59	colonial	0	0	DC	716000	5327000
L72	solitary	0	0	DC	715852	5294180
L65	solitary	0	0	DC	715200	5294250
L73	solitary	0	0	DC	715097	5294460
L66	solitary	0	0	DC	701550	5297600
L75	solitary	0	0	DC	707520	5298610
L74	solitary	0	0	DC	708138	5301376
L76	solitary	0	0	DC	709900	5311950
L71	solitary	0	0	DC	710867	5318467
L61	solitary	0	0	DC	722200	5306500

ID #	colonial/solitary	No. fledged (2001)	No. fledged (2002)	Site	MTUe	MTUn
L62	solitary	0	0	DC	710035	5312949
UR38	colonial	0	0	IP	714300	5330000
L39	colonial	0	0	L CW	714800	5328100
L56	solitary	0	0	LC	707228	5306041
L68	solitary	0	0	PF	713241	5328746
L69	solitary	0	0	PF	712606	5329164
L70	solitary	0	0	PF	709667	5329275
L67	solitary	0	0	PF	714703	5329542
UR43	colonial	0	0	TP	714100	5328200
L27	colonial	0	0	TP	714600	5329050
UR44	colonial	0	0	TP	715010	5329500
UR42	colonial	0	0	TP	714900	5329800
UR40	colonial	0	0	TP	712400	5331050
L64	solitary	0	0	TP	708700	5309900
L63	solitary	0	0	TP	705426	5326641
UR50	solitary	0	0	TP	707050	5329100
UR45	solitary	0	0	TP	710450	5329800
UR37	solitary	0	0	TP	707800	5334600